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Bat community structure in South America: a tenacious chimera

Estructura comunitaria de murciélagos en Sudamérica: una quimera tenaz

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ABSTRACT

Although bats make a disproportionately large contribution to the increase in mammalian species richness as one proceeds toward the equator (Wilson 1974), little is known about the composition or structure of Neotropical bat communities. Most characteristics of Neotropical bat communities have been deduced from larger faunal surveys. Only two bat communities from mainland South America have been intensively studied (the Caatingas and edaphic Cerrado communities of northeast Brazil). Thus, comparisons of bat community ecology must await additional long-term studies of bats at the level of local communities. The major distinction between Caatingas and edaphic Cerrado communities concerns the importance of frugivores and foliage-gleaning insectivores. Frugivores dominate the Cerrado fauna whereas a more homogeneous array of importance values characterizes the Caatingas. The theoretical and practical limitations of guild-size niche matrices are also explored. These matrices obscure more information than they reveal concerning Caatingas or edaphic Cerrado bat community organization. Numerous niche cells are multiply occupied and the majority are empty. Moreover, species in adjacent cells may be more similar than the species in the same cell. Correlation analysis suggests that size is an important consideration in structuring these communities: the size ratio of adjacent species increases as the size of the potential competitors increases. Whether this pattern is a result of biotic interactions or is a statistical artifact remains to be evaluated.

Key words: community structure, competition, limiting similarity, guild, Chiroptera, Neotropics, Caatingas, Cerrado.

RESUMEN

Aunque los murciélagos contribuyen en forma desmesurada al incremento en la riqueza específica de mamíferos a medida que se procede hacia el ecuador (Wilson 1974), poco es lo que se sabe acerca de la composición o estructura de las comunidades de murciélagos neotropicales. La mayoría de las características de dichas comunidades se han deducido a partir de catastros faunísticos. Sólo dos comunidades de murciélagos han sido intensamente estudiadas en Sudamérica continental (en la Caatinga y el Cerrado edáfico del noreste de Brasil). En consecuencia, las comparaciones de estructura comunitaria de murciélagos deberán esperar la realización de más estudios de larga duración al nivel de comunidades locales. Las mayores diferencias entre las comunidades de murciélagos de Caatinga y Cerrado edáfico conciernen a la importancia de frugívoros e insectívoros buscadores en dosel. Los frugívoros dominan la fauna del Cerrado en tanto que la Caatinga se caracteriza por una distribución más homogénea de los valores de importancia. Se exploran las limitaciones teóricas y prácticas de las matrices de nicho gremial. Estas matrices oscurecen más información de la que revelan acerca de la organización comunitaria de murciélagos en la Caatinga o el Cerrado edáfico. Numerosas celdas de nicho están ocupadas en forma múltiple y la mayoría están vacías. Además, las especies en celdas adyacentes pueden ser más similares entre ellas que con especies en la misma celda. Análisis de correlación sugieren que el tamaño corporal es un factor importante en la estructuración de estas comunidades de murciélagos: el cociente de tamaño entre especies contiguas aumenta a medida que el tamaño corporal de los competidores potenciales aumenta. Si este patrón es el resultado de interacciones bióticas, o un artefacto estadístico, queda por ser evaluado.

Palabras claves: estructura comunitaria, competición, similaridad limitante, gremio, Chiroptera, Neotrópicos, Caatingas, Cerrado.

INTRODUCTION

A community is an association of potentially interacting species-populations and is defined primarily by the nature of the interactions and by the place where they occur (Ricklefs 1979). The fundamental niche of a species-population reflects inherent tolerance limits whereas the realized niche accounts for subsequent modification in response to the biotic environment. By definition, the realized niche only has meaning within the context of the community. Hutchinson's (1959) formalized de-

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finition of the niche as an n-dimensional hypervolume synthesized aspects of population biology and community ecology, and redirected many aspects of ecological research. The total resource base of a community may be viewed as an n-dimensional hypervolume. The portion of this total hypervolume occupied by a particular species is its niche. Differences in the composition of two communities can then be attributed to differences in the total resource base of each area, or to the manner in which species are organized within the total hypervolume, or to historical differences (speciation/extinction) between the two communities. Obviously, the delineation of all the variables and interactions defining a species' niche is not feasible. Recognizing this limitation, ecologists have focused their attention on the degree to which the niches of two species overlap as measured by some limited but important subset of variables. Measures of overlap are typically based upon a variety of characteristics including diet composition, microhabitat, foraging strategy, and period of activity (Schoener 1968, 1974, Pianka 1973, Cody 1974, Brown 1975). Some dimensions may be continuous variables whereas others are clearly discontinuous. Moreover, Schoener (1974) has pointed out that even continuous variables do not necessarily provide equal ecological opportunities throughout their range. Roughgarden (1974) cautions that the ecological niche breadth of a population is greater than that of any single individual and that a between-individual component of niche breadth must be considered in a realistic assessment of a population's niche. In addition, daily and seasonal changes in activity patterns alter the niche of an organism such that intra-community relations may change with time also (Ricklefs 1979). Complicating matters further, the ecological overlap between species is defined with respect to a particular habitat for each taxon. Differences in feeding categories, behavioral attributes, and assessed microhabitat characteristics differ for different kinds of species and habitats, and as such, measures of niche breadth are not necessarily comparable even if the utilized mathematical algorithms are the same (Ricklefs & Travis 1980). One possible solution to these problems, lies in ecomorphological analyses. Ecologists increasingly have used morphological characteristics to infer ecological attributes (cf. Findley 1973, 1976, Mares 1975, 1976, 1980; Karr & James 1975, Ricklefs & Travis 1980). Ecomorphological analyses assume that the niche relationships of species in a community are reflected in their morphological adaptations (Ricklefs 1979). Environmental parameters impose restrictions on the phenotypes of organisms within a particular habitat; those phenotypes that successfully reproduce in an environment are adaptative by definition; and adaptation ought to be reflected in the morphological and ecological attributes which constitute the phenotype.

The central questions in community ecology deal with the factors accounting for the select and restricted group of species found within a particular habitat. In ecomorphological terms, the question becomes, do species exhibit morphological patterns within communities that imply certain ecological processes that limit the species composition of communities?

Some success in distinguishing ecological niches within a fauna has been obtained by looking at a few morphological characteristics. Fenton (1972) has shown that the increased species richness observed in the chiropteran fauna of Cameroun as compared to the bat fauna of southeastern Ontario is primarily due to an increase in the area of occupied morphological space (determined by the ratio of ear length to forearm length and the ratio of the lengths of third to the fifth digit). Although criticized on technical grounds by Ricklefs & Travis (1980), Findley (1973, 1976) corroborated Fenton's findings based upon a multivariate analysis of chiropteran faunal regions; high species richness in faunal regions appears to be accomplished by increasing the variety of ecomorphological types (increased size of morphological space) rather than by decreasing the distance between neares neighbors. Analyses of large bird faunas by Karr & James (1975) and of different bird communities by Ricklefs & Travis (1980) yield similar conclusions concerning the relation between species packing and species richness. The work of Fenton (1972) and Findley 1973, 1976), however was not designed to detect ecomorphological patterns in bat *communities;* rather their work focused on a higher level of organization (e.g., continents and countries). Similarly, the analyses of Karr & James (1975) and Moulton

& Pimm (1986) were not restricted to particular avian communities; rather, they examined species composition and structure within biomes or islands potentially containing a number of different communities. I believe that these analyses have failed to distinguish the composition or structure of the component communities. On the other hand, the analysis of Ricklefs & Travis (1980) is unique because multivariate ecomorphological patterns were examined within delimited bird communities. However, the understanding of *community* organization in the Chiroptera cannot simply be deduced from analyses of continental bat faunas or from analyses of different taxa (birds).

Although community ecology includes a variety of research areas and approaches, a common basis ought to be a focus at the organizational level of biological communities – locally interacting groups of organisms. It seems axiomatic then, that studies of Neotropical bat communities in South America ought to be focused on local assemblages where *in situ* ecological processes (competition, predation, mutualism, parasitism, resource availability, etc.) affect the taxonomic composition and ecomorphological structure. Nonetheless, much of our understanding of South America bat communities is based on studies that deal with levels of organization above the community. Indeed, the companion paper in this volume by Fleming illustrates the kinds of data and interpretations that may be derived from studies of faunal composition at the level of islands (in the Caribbean) and phytogeographic regions (of Venezuela). These studies make valuable contributions to our understanding of evolutionary or biogeographic processes or patterns that are manifested above the level of communities. They may also provide insight into understanding community patterns and processes. However, the nature of the filtration process from supra-community level to community level is subject to criticism from a variety of viewpoints (see Allen & Starr 1982 and references therein) and rekindles the reductionism-holism controversy.

Caution must be exercised in interpreting conclusions applied to communities when confounding effects (e.g., habitat diversity, β-diversity, island area and distance to faunal pools) have not been controlled in a rigorous fashion. Of the six Neotropical bat communities considered by Fleming in this volume, only two (the Caatingas and edaphic Cerrado site in northeast Brazil) occur on the mainland of South America. Additional research at the level of local communities, both within and among habitat types, will provide the necessary data for the development of a truly comparative science at the level of ecological communities.

Three questions that need to be addressed before a solid understanding of the structure of South American bat communities becomes evident are: 1) Do local bat communities exhibit a structure (i.e., patterns in composition)? 2) How ubiquitous are those patterns? 3) What are the determinants of those patterns? The intent of this paper is to evaluate data from South American bat communities as they pertain to these questions and provide a framework upon which to base future comparisons.

AN ORGANIZATIONAL PARADIGM

In the absence of detailed information on species-species interactions, guild-size matrices have commonly been employed by bat ecologists to reveal the extent of organization (McNab 1971, Fleming *et al.* 1972, Wilson 1973, Smith & Genoways 1974, LaVal & Fitch 1977) at both community and supra-community levels. Bat species are classified into guilds (groups of species which consume similar foods via similar foraging techniques; *sensu* Root 1967) wherein competition is believed to play a significant role in determining guild composition (see Pianka 1980 and references therein). Jaksić (1981) provides a concise overview of the concept of guilds in community ecology. Within feeding guilds, species are further differentiated by size. The assumption is that guild membership is accurately ascertained for each species and that competition for food (or some other limiting resource) restricts guild membership according to size-related assembly rules.

Guild Determination

The typical feeding associations incorporated in niche matrices include: piscivory, sanguinivory, aerial insectivory, foliage-gleaning insectivory, nectarivory, frugivory, and omnivory (McNab 1971). The fixed nature of this classification scheme is problematic when guild membership is primarily obtained from the literature. The food habits of many phyllostomids are diverse geographically and temporally. The summary work of Gardner (1977) indicates the paucity of food habit data available for most phyllostomids. Diets of other South American taxa are even less well documented. Moreover, bats for which data are available in the subfamilies Phyllostominae and Glossophaginae consume fruit, insects, flower parts, and sometimes vertebrates. Their classification into single guilds without knowledge of local feeding habits within a community is tenuous at best. To reiterate, the value of niche matrices is predicated upon accurate determination of food habits in local communities and such data are lacking for South America except in edaphic Cerrado or Caatingas communities (Willig 1982, 1983, 1985a).

Size Categories

The basic assumption that competition determines the structure of bat communities is reflected by the use of Hutchinson's ratio to delineate the size categories in niche matrices. In fact, size categories have been constructed such that upper endpoints of adjacent categories differ by a factor of 1.26. The utility of Hutchinson's ratio has been questioned on theoretical terms (Bossert 1963, Maiorana 1978, Roth 1981); moreover, Simberloff and Boecklen (1981) have statistically reanalyzed a large number of data sets (including vertebrate and invertebrate taxa) and have concluded that Hutchinson's ratio has outlived its usefulness in evolutionary biology. Wiens (1982) provides a cogent summary concerning the status of size ratios in ecology and suggests appropriate methodologies for resolving the controversy. It never has been empirically evaluated within South American chiropteran communities. Moreover, Abrams (1983) has questioned the theoretical underpinnings of limiting similarity in general. Such objections aside, the use of size categories is questionable because species occupying different niche cells may be more similar than 1.26. As a consequence, species within the same niche cell may be more dissimilar than two species, each occupying a different cell.

The composition of two well-delimited bat communities in northeast Brazil (Willig 1982, 1983) provides unique opportunities for examining the utility of niche matrices as estimators of community organization. The question of whether or not local communities exhibit a structure determined by random processes has become increasingly important (see Ricklefs & Travis 1980, Ricklefs *et al.* 1981, Bowers & Brown 1982) and is considered elsewhere (Willig & Moulton, unpubl.)[1] for these Brazilian bat communities.

MATERIAL AND METHODS

Faunal Composition

Bats were collected by netting from September 1976 to May 1978 in Caatingas (Municipality of Exu, Pernambuco) and edaphic Cerrado (Chapada do Araripe, Municipality of Crato, Ceará) habitats in northeastern Brazil (Fig. 1). Because I was interested in determining the composition of a local community within the Caatingas and within the Cerrado, only monthly samples from a restricted area were utilized in subsequent analyses. Sampling locales were contained within a circular area with a radius of 10 km in each biome. Five to ten locales in each biome were visited each month. Standard Japanese nylon mist nets (10 m x 2 m) were used to collect specimens. Although the position of the nets was determined by peculiarities of the terrain and the physiognomy of the vegetation, I was usually able to erect 10 sections of netting per night in the most frequented collection sites. All nets were positioned before dusk and checked at fifteen minute intervals or sooner depending upon the level of bat activity. Because activity usually was quite high at most collection sites, the nets were, in effect, monitored continuously. Nets remained open for a minimum of 3.5 to 4 hours each night. Initial field work indicated that additional netting was counter-productive; total activity diminished drastically after 2100-2130 hours and more importantly, no additional species were caught during later time periods. Supplemental collecting from roosts (e.g., caves, tree hollows, buildings, culverts, etc.), was done in order to verify that the faunal

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[1] WILLIG MR & MP MOULTON (unplub.). Are northeast Brazilian bat communities randomly assembled?

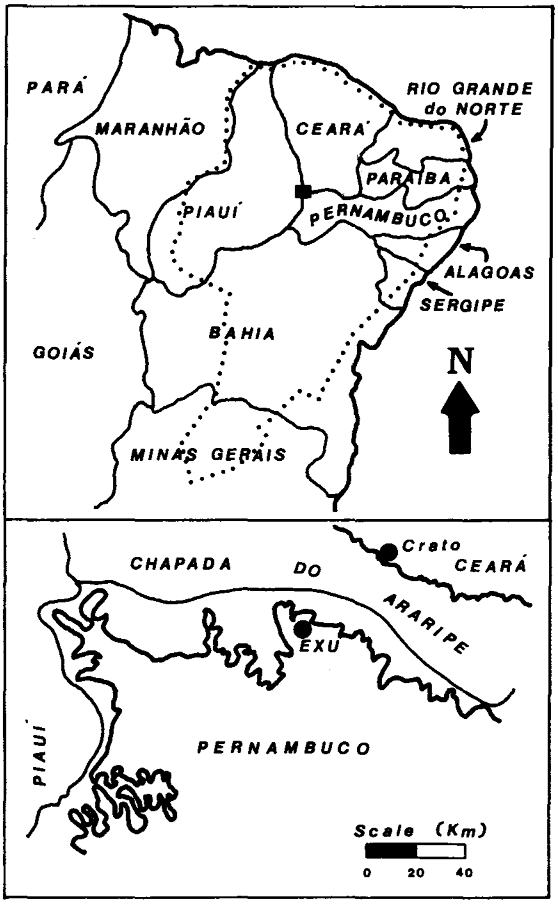

Fig. 1. The Caatingas (delimited by the dotted line in the upper frame) occupies over 650,000 km^2 and is contained within nine states of the Brazilian Northeast. Because of its irregular shape and susceptibility to extended periods of drought, the region is known as "o polígono das secas" (the polygon of drought). The solid rectangle indicates the location of the study sites. The proximity of Caatingas (Exu, Pernambuco) and edaphic Cerrado (Crato, Ceará) habitats, and their relation to the Chapada do Araripe are indicated in the lower frame. Modified after Willig (1985b).

La Caatinga (delimitada por la línea punteada en la parte superior de la figura) ocupa cerca de 650.000 km^2 y queda comprendida dentro de nueve estados del noreste del Brasil. Debido a su forma irregular y susceptibilidad a largos períodos de sequía, la región es conocida como "o polígono das secas" (el polígono de las sequías). El rectángulo negro indica la localización de los sitios de estudio. La proximidad de hábitats de la Caatinga (Exu, Pernambuco) y de Cerrado edáfico (Crato, Ceará) y su relación con la Chapada do Araripe se indica en la parte inferior de la figura. (Modificado de Willig 1985b).

composition was not biased by collecting techniques. Specimens are housed in the Carnegie Museum of Natural History, Section of Mammals (Pittsburgh, Pennsylvania, USA) and O Museu de Zoologia da Universidade de São Paulo, Seção de Mamíferos (São Paulo, Brazil).

Community Determination

Although some bat species are capable of dispersing long distances, it is unlikely that individual ranges would frequently span the 40 km distance between Caatingas and edaphic Cerrado sites. Moreover, the intervening habitats between Exu and Crato on the southern edge of the Chapada do Araripe are highly disturbed (pasture or pineapple plantation); netting yielded very few individuals, all of which were *Artibeus jamaicensis.* The Caatingas site is a mosaic of habitats (Caatinga Alta, Caatinga Baixa, Serrotes, and Lajeiros) which interdigitate in such a fashion that discrete populations of any bat species are unlikely to be confined to a particular habitat. In fact, roosting sites for most species occur on Serrotes. Even species which seem to prefer Caatinga Alta (*Mimon crenulatum, Micronycteris megalotis, Micronycteris minuta* and *Tonatia brasiliense*) or Lajeiros (*Neoplatymops mattogrossensis*) may roost in Serrotes. Thus, it seems reasonable and practical to consider the bat species which co-occur within the 10 km radius of Exu to compose a single community of syntopic species, even though habitats within that area are heterogeneous.

Feeding Guild Determination

Species of bats from Caatingas and edaphic Cerrado habitats were categorized into feeding guilds based upon a consideration of three criteria: 1) the qualitative analysis of the contents of fecal samples obtained from specimens in the field; 2) the qualitative analysis of stomach contents determined in the laboratory from recently sacrificed specimens; and 3) reference to the work of Wilson (1973) and Gardner (1977). McNab (1971) classified bats into six feeding guilds: frugivores, nectarivores, insectivores, carnivores, piscivores, and sanguinivores. Wilson (1973) used a similar classification except that he divided the insectivore guild of McNab into foliage gleaners and aerial insectivores; most subsequent workers have utilized Wilson's categorization in their analysis of bat feeding guilds and I initially conformed with that convention in examining guild composition of bats in northeast Brazil. However, it quickly became apparent that the aerial insectivore guild was morphologically quite heterogeneous (Willig 1982) and that these differences appeared to be reflected in foraging strategies. The utilization of the molossid aerial insectivore guild as a separate entity reflects the ecological position of the component species as analogs of swifts and swallows (Vaughan 1966, 1970), and results in the following evaluation being conservative (i.e., it makes it more difficult to reject the utility of the niche matrix paradigm).

Community Structure

The bat faunas from Exu, Pernambuco and Crato (Floresta Nacional Araripe-Apodí) Ceará were considered separately in order to assess the structure of the chiropteran communities in Caatingas and edaphic Cerrado habitats of northeast Brazil. Two-dimensional niche matrices (after Fleming *et al.* 1972) based upon size and feeding guild membership were used as first-approximations to community structure in each biome. Forearm length was used as the general indicator of size because it is less susceptible to temporary fluctuations caused by reproductive condition, season, and stomach contents; is highly correlated with all other linear measures of size (see Willig 1983); and would facilitate comparison with previous studies that also used forearm length. The Importance Value of each guild reflects its proportional contribution to species richness in the community and was calculated as the percent of the total species pool in the community represented by a particular guild (Smith & Genoways 1974).

Finer resolution of the body size relations within each guild were attempted via statistical analysis conforming for the most part with the suggestions of Wiens (1982). The forearm lengths for each bat species were obtained from Willig (1983) and used to calculate 95% confidence intervals (Sokal & Rohlf 1981). Adult males and females were considered together in order to incorporate the natural morphometric variation of the species into an estimate of mean forearm length. When geographic variation for a species was not detected by the Analysis of Variance (see Willig 1983), samples from the Caatingas and edaphic Cerrado habitats were combined in order to estimate forearm size more reliably. If geographic variation was statiscally significant, forearm data were not pooled; thus Caatingas and Cerrado populations of the same species can have different estimates of mean forearm size. In a sense, sexual dimorphism is ignored in determining size ratios; however, if a species is dimorphic, that condition should increase measures of variation for forearm length and would make it more difficult statistically to reject the constant Hutchinsonian size hypothesis. Moreover, the evaluation of what constitudes size dimorphism is not simple (see Willig *et al.*, 1986) yet the effect of any statistical or ratio analysis would be predicated on the correct evaluation of dimorphism. Confidence intervals were then plotted in ascending rank order according to mean forearm size for all common species within each guild. In addition, a modification of the Behrens-Fisher *t'* test (Snedecor & Cochran 1967, Roth 1981) was used to determine if the ratio of mean forearm size between adjacent bat species differed statistically from the Hutchinsonian value of 1.26 (Hutchinson 1959).

RESULTS AND DISCUSSION

Faunal Composition

More than five thousand bats representing thirty-eight species, twenty-nine genera, and eight families were captured during this study (65% of the mammalian species known from the Exu-Crato area are members of the Chiroptera, see Mares *et al.* 1981). Table 1 lists the bat species from this study in systematic order, indicates their relative abundance in Caatingas or edaphic Cerrado habitats (based upon netting records), and defines their feeding guild associations. Twenty species are shared between areas; further, the Caatingas contains thirteen species not found in the Cerrado, whereas the Cerrado contains five species not found in the Caatingas. If only the non-rare species in each biome are considered, the dissimilarities between areas become more pronounced: fifteen of the twenty-four species (over half of the species pool) occur exclusively in one or the other of the areas. Despite geographic proximity, the Caatingas and edaphic Cerrado habitats contain markedly different bat faunas.

Faunal composition and species densities are uniform in edaphic Cerrado habitats on the Chapada do Araripe. Conversely, the Caatingas is quite heterogeneous in this regard. Caatinga Baixa (low-lying thorn scrub) contains few species of bats, and those species present occur ar very low densities. Lajeiros (lowlying granitic outcrops) contain a few additional species (*Neoplatymops mattogrossensis*) (see Willig 1985b) and *Peropteryx macrotis,* but in general, the fauna of the Caatingas in low-lying areas (Caatinga Baixa and Lajeiros) is depauperate. Species of foliage gleaning insectivore (*Mimon crenulatum, Micronycteris megalotis, Micronycteris minuta* and *Tonatia brasilense*) reach their highest density and occur almost exclusively in Caatinga Alta (semideciduous drought-adapted forest). With few exceptions, however, Serrotes (granitic mountains) harbor the bulk of the species found in the Caatingas, and it is on Serrotes or the adjacent areas of Caatinga Alta that most species reach their highest densities. As such, the relatively high species richness of the Caatingas can be attributed in part to the topographic relief and vegetational diversity of the Caatingas, but more importantly from the point of view of the Chiroptera, the numerous Serrotes that punctuate the flat landscape of the Caatingas provide roosting sites and mesic refugia during drought periods (Streilein 1982, Willig 1982, Mares *et al.* 1985).

TABLE 1

Systematic listing of bats from Caatingas (Exu, Pernambuco) and Cerrado (Crato, Ceará) biomes; A indicates abundant, C indicates common, R indicates rare, and – indicates absent. Feeding guild abbreviations: AERIN, aerial insectivore; PISCI, piscivore; FOLGL, foliage-gleaning insectivore; OMNIV, omnivores; NECTA, nectarivores; FRUGI, frugivore; SANGU, sanguinivore; MOLOS, molossid aerial insectivore.

Lista sistemática de los murciélagos de los biomas de Caatinga (Exu, Pernambuco) y de Cerrado (Crato, Ceará). A indica abundante, C indica común, R indica raro, – indica ausente. Las abreviaturas para gremios tróficos significan: AERIN, insectívoro aéreo; PISCI, piscívoro; FOLGL, insectívoro buscador en dosel; OMNIV, omnívoro; NECTA, nectarívoro; FRUGI, frugívoro; SANGU, sanguinívoro; MOLOS, insectívoro aéreo molóssido.

		PRESENCE		
	SPECIES	CAATINGAS	CERRADO	GUILD
Family	Emballonuridae			
	Saccopteryx leptura	–	R	AERIN
	Peropteryx macrotis	C	–	AERIN
Family	Noctilionidae			
	Noctilio leporinus	C	R	PISCI
Family	Mormoopidae			
	Pteronotus davyi	R	R	AERIN
Family	Phyllostomidae			
Subfamily	Phyllostominae			
	Micronycteris megalotis	R-C	R	FOLGL
	Micronycteris minuta	R-C	R	FOLGL
	Tonatia bidens	R	–	FOLGL
	Tonatia brasiliense	R-C	–	FOLGL
	Tonatia silvicola	C	–	FOLGL
	Mimon crenulatum	R-C	–	FOLGL
	Phyllostomus discolor	R-C	A	OMNIV
	Phyllostomus hastatus	R	A	OMNIV
	Trachops cirrhosus	C	–	OMNIV
Subfamily	Glossophaginae			
	Glossophaga soricina	A	A	NECTA
	Lonchophylla mordax	C	–	NECTA
	Anoura geoffroyi	R	C	NECTA

Cuadro 1 (Cont.)

		PRESENCE		
	SPECIES	CAATINGAS	CERRADO	GUILD
Subfamily	Carolliinae			
	Carollia perspicillata	A	A	FRUGI
Subfamily	Stenodermatinae			
	Sturnira lilium	R	C-R	FRUGI
	Uroderma magnirostrum	R	R	FRUGI
	Vampyrops lineatus	A	A	FRUGI
	Artibeus concolor	–	C-R	FRUGI
	Artibeus jamaicensis	C	A	FRUGI
	Artibeus lituratus	C-R	A	FRUGI
Subfamily	Desmodontinae			
	Desmodus rotundus	A	R	SANGU
	Diphylla ecaudata	R	–	SANGU
Family	Natalidae			
	Natalus stramineus	–	R	AERIN
Family	Furipteridae			
	Furipterus horrens	R	–	AERIN
Family	Vespertilionidae			
	Myotis nigricans	C-A	C	AERIN
	Eptesicus furinalis	–	C-R	AERIN
	Lasiurus borealis	–	R	AERIN
	Lasiurus ega	R	R	AERIN
Family	Molossidae			
	Molossops planirostris	R	–	MOLOS
	Molossops temminckii	R	R	MOLOS
	Tadarida laticaudata	R	R	MOLOS
	Neoplatymops mattogrossensis	C	–	MOLOS
	Molossus ater	R	–	MOLOS
	Molossus molossus	A	A	MOLOS
	Eumops sp.	R	–	MOLOS

Niche Matrices, Hutchinson's Ratio, and Competitive Interactions

Niche matrices are based upon the principle of limiting similarity (MacArthur & Levins 1967): Potential competitors, members of the same feeding guild, must differ from each other in the use of resources in order to coexist within the same community (see Wilson 1975 and Abrams 1983 for cogent critiques of the theoretical and empirical bases of the concept). A minimum size value is utilized because the variation in size among different consumers is frequently correlated with variation in size of their food (Baker & Baker 1936, Van der Pijl 1957, Ashmole 1968, Brown 1973, 1975, Mares & Williams 1977). Thus, each cell in a niche matrix should be occupied by only one common species (McNab 1971). Hutchinson (1959) suggested that a size differential of 1.26 was a *tentative* (my emphasis) indication of the magnitude of difference necessary to permit the coexistence of potential competitors in the same feeding guild, and this value has apparently become fixed as the size ratio used to construct guild matrices. However, species in adjacent niche cells may actually be different from each other by a factor much less than 1.26 (in fact, the ratio could be 1.01 or even smaller). Numerous other studies have adopted the 1.26 ratio as a biological constant (cf. Klopfer & MacArthur 1961, Price 1972, Robinson 1971, May 1974, Horn & May 1977, Van Valen

1978) with larger or smaller ratios indicative of the importance of food size in distinguishing niche structure (cf. Fleming *et al.* 1972).

Contrary to expectations, numerous unoccupied niche cells characterize both Caatingas and edaphic Cerrado communities (Table 2 and 3). Similar results have been obtained by McNab (1971), Smith & Genoways (1974), and LaVal & Fitch (1977) for other bat assemblages. McNab (1971) has suggested that these "empty cells" are actually filled by species of intermediate or rare occurrence. This is undoubtedly true to some extent in communities which have been inadequately surveyed or for supra-community level analyses; however, the local communities from both Caatingas and edaphic Cerrado habitats have been extensively surveyed and the inclusion of all bat species regardless of their abundance in the Caatingas and Cerrado analyses does not appreciably alter the general conclusion that many niche cells are unoccupied. Vacant niche cells may reflect peculiarities of food size distributions within the community. For example, foods at the large end of the size gradient may be less abundant than smaller foods, so that larger consumer species must exploit foods distributed over a wider range of sizes. On the other hand, diffuse competition within the Chiroptera or competition by taxa outside the bat fauna (Fenton & Fleming 1976, Fleming 1979) may effectively occupy these apparently empty niche cells. Discrimination among the alternatives is not possible based upon the results of this study; however, the potential for diffuse competition among bats in different feeding guilds is quite high. Nectarivores often consume fruit and insects in addition to nectar and pollen; foliage gleaners consume fruit and insects; omnivores consume fruit, insects and vertebrate flesh (Gardner 1977); even piscivores consume insects in addition to fish (Willig 1982). It seems highly likely then that some of the vacant cells in the niche matrix are actually occupied to some extent by euryphagic species; however, documentation of this needs to include detailed analysis of stomach contents before such a statement can be accepted with a greater degree of confidence.

TABLE 2

Niche matrix for the bat community from the Caatingas of northeast Brazil. Importance values (IV) have been calculated according to the method of Smith & Genoways (1974). Base entries represent IVs determined by restricting consideration to the common species in each guild; values in parentheses represent IVs determined from the species pool regardless of abundance. Species numbers within the body of matrix consider only common species; the parenthetical values indicate the additional number of uncommon species occurring within a particular niche matrix cell. Guild codes defined in Table 1.

Matriz de nicho para la comunidad de murciélagos de la Caatinga en el noreste de Brasil. Los valores de importancia (IV) se calcularon de acuerdo al método de Smith & Genoways (1974). Los valores de IV fuera de paréntesis están computados considerando sólo las especies comunes de cada gremio; aquellos entre paréntesis están computados en base a todas las especies integrantes de cada gremio, independientemente de su abundancia. Los números de especies consignados fuera de paréntesis en la matriz corresponden sólo a las especies comunes; aquellos entre paréntesis consignan el número de especies no comunes que integran una celda gremial particular. Los códigos de los distintos gremios aparecen en la Tabla 1.

		NUMBER OF SPECIES DISTRIBUTED BY FOREARM LENGTH (MM)							
GUILDS	IV	≤29	30-34	35-43	44-54	55-68	69-86	≥ 87	TOTAL
PISCI	.05(.03)						1		1
SANGU	.05(.06)				0 (1)	1			1(1)
OMNIV	.15(.09)					2	1		3
NECTA	.10(.09)			2	0 (1)				2(1)
FRUGI	.20(.18)			1(1)	1 (1)	1	1		4(2)
FOLGL	.25(.18)		2	1	1	1 (1)			5(1)
AERIN	.10(.15)		1 (1)	1	0 (2)				2(3)
MOLOS	.10(.15)		1 (2)	1 (2)		0 (1)			2(5)
TOTAL		0	4 (3)	6 (3)	2 (5)	5 (2)	3	0	20 (13)

TABLE 3

Niche matrix for the bat community from the edaphic Cerrado of northeast Brazil. Importance values (IV) have been calculated according to the method of Smith & Genoways (1974). Base entries represent IVs determined by restricting consideration to the common species in each guild; values in parentheses represent IVs determined from the species pool regardless of abundance. Species numbers within the body of matrix consider only common species; the parenthetical values indicate the additional number of uncommon species occurring within a particular niche matrix cell. Guild codes defined in Table 1.

Matriz de nicho para la comunidad de murciélagos del Cerrado edáfico en el noreste de Brasil. Los valores de importancia (IV) se calcularon de acuerdo al método de Smith & Genoways (1974). Los valores de IV fuera de paréntesis están computados considerando sólo las especies comunes de cada gremio; aquellos entre paréntesis están computados en base a todas las especies integrantes de cada gremio, independientemente de su abundancia. Los números de especies consignados fuera de paréntesis en la matriz corresponden sólo a las especies comunes; aquellos entre paréntesis consignan el número de especies no comunes que integran una celda gremial particular. Los códigos de los distintos gremios aparecen en la Tabla 1.

		NUMBER OF SPECIES DISTRIBUTED BY FOREARM LENGTH (MM)							
GUILDS	IV	⩽ 29	30-34	35-43	44-54	55-68	69-86	⩾ 87	TOTAL
PISCI	.00(.04)						0 (1)		0 (1)
SANGU	.00(.04)					0 (1)			0 (1)
OMNIV	.15(.08)					1	1		2
NECTA	.15(.08)			2					2
FRUGI	.46(.28)			2	2 (1)	1	1		6 (1)
FOLGL	.00(.08)		0 (2)						0 (2)
AERIN	.15(.28)		1	1 (3)	0 (2)				2 (5)
MOLOS	.08(.12)		0 (1)	1 (1)					1 (2)
TOTAL		0	1 (3)	6 (4)	2 (3)	2 (1)	2 (1)	0	13 (12)

The occurrence of multiply occupied niche cells in the Caatingas and edaphic Cerrado communities is more problematic because it suggests that the utilization of Hutchinson's ratio as the measure limiting similarity is invalid. One nectarivore cell and two frugivore cells are each occupied by two common species in the Cerrado (Table 3) whereas one nectarivore, frugivore, and omnivore cell is each occupied by two common species in the Caatingas (Table 2). When all species are considered regardless of abundance, up to four species occupy a single cell (35-43 mm aerial insectivore) in the Cerrado; in both communities, the majority of occupied cells contain two or more species. This suggests that food resources may not be limiting factors within particular niche cells or that bats do not primarily discriminate among possible dietary components based upon size considerations.

Alternatively, the niche matrix methodology may obscure important size differences within the fauna by arbitrarily delimiting the location of categories along the size dimension. Size categories are ostensibly a reflection of the mathematical consequences of the theory of limiting similarity, where each category differs from adjacent categories by a factor of 1.26 in linear measurements or 2.0 in volumetric or weight measurements. The range of forearm length used by McNab (1971) to define bat food-size niches has become "standard" in the literature. He apparently constructed his categories such that the end points of each category differed by a factor of roughly 1.26 (e.g., 43 = 1.26 x 34; 54 = 1.26 x 43, etc.). As a result of that arrangement, the mid-points in each category do not vary by a factor of 1.26 and, indeed, they could not in any scheme of this type. Further, using 30 to 34 as the first category has no inherent advantage over using 28.6-36.0, and yet the conclusions drawn from analyzing data by these slightly different methods could be quite different.

As an alternative approach, I examined the size relations among species within the same guild using a simple statistical methodology, that conforms, for the most part, to the criteria of Wiens (1982) and that does not depend upon an *a priori* classification of species into particular size categories. Ninety-five percent confidence intervals of the mean were chosen as a manner to express the niche size of a particular species and a rigorous statistical criterion was established to ascertain the validity of a consistent size separation between species in the same guild. The criterion requires ratios of forearm lengths between adjacent bat species to be statistically different and adjacent sizes of bats to have mean values which differ by a factor of 1.26. Figures 2 through 7 illustrate the size relations among bats in the omnivore, nectarivore, frugivore, foliage gleaning insectivore, aerial insectivore, and molossid insectivore guilds, respectively. The piscivore and sanguinivore guilds each contain a single common species, and are not shown.

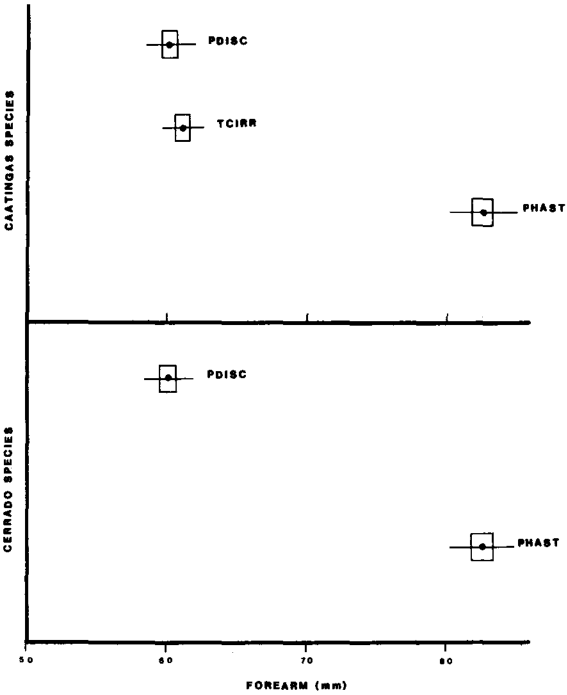

Fig. 2. Size relations among omnivorous species in Caatingas and edaphic Cerrado communities. Mean forearm size is indicated by a solid dot; 95% Confidence Intervals for mean forearm size are indicated by open horizontal bars; individual variation in forearm size (x̄ ± 1SD) is indicated by a solid horizontal line. Size ratios based upon x̄) for successive pairs of species beginning at the left of the x-axis are 1.01 and 1.35 in the Caatingas, and 1.37 in the Cerrado. Species codes: PHAST = *Phyllostomus hastatus*, TCIRR = *Trachops cirrhosus*, PDISC = *Phyllostomus discolor.*

Relaciones del tamaño corporal entre especies de murciélagos omnívoros de la Caatinga y el Cerrado edáfico. El tamaño medio del antebrazo se indica con un círculo negro; el intervalo de confianza del 95% en torno a la media para tamaño del antebrazo se indica con una barra horizontal; la variación individual en el tamaño del antebrazo (x̄ ± 1 DE) se indica con una línea horizontal. Los cocientes de tamaño (basados en x̄) para pares de especies contiguas a partir del origen del eje de abscisas son: 1.01 y 1.35 en la Caatinga y 1.37 en el Cerrado. Códigos específicos: PHAST = *Phyllostomus hastatus*, TCIRR = *Trachops cirrhosus*, PDISC = *Phyllostomus discolor.*

The importance values for each guild appear in Tables 2 and 3. The major differences between Caatingas and edaphic Cerrado bat communities are associated with the importance of frugivores and foliage gleaners. When considering only common species, the edaphic Cerrado community is dominated by frugivores, whereas the Caatingas community has a more homogeneous distribution of importance values among guilds. Further, the foliage gleaners are important components in the Caatingas while being relatively minor components of the edaphic Cerrado community, even when rare species are included in the analysis.

In all but three cases, the 95% confidence intervals for mean forearm size of common bats do not overlap within guilds. Further, there appears to be little overlap in size between species even if the broader measures of individual variation (X̄ ± 1SD) are utilized. In general, there clearly seem to be discrete size gradations within feeding guilds which are obscured by the niche-matrix analysis. This pattern could, however, be a spurious result of the size distribution of extant bats which compose the species pool (i.e., the random selection of bat species from a limited species pool could give rise to a similar pattern). The question remains, however, if the Hutchinsonian value of 1.26 is a meaningful constant in bat communities.

Roth (1981) and Wiens (1982) summarize the theoretical and empirical evidence which pertains to the existence of constant size ratios within groups of competing species. Hutchinson's (1959) original suggestion of the 1.26 ratio was based upon empirical deductions made from 13 observed ratios in a disparate group of species which included insects, birds, and mammals. The actual 1.26 value is the mean of the ratios he observed which in fact varied from 1.1 to 1.4. Bossert (1963), Schoener (1965, 1974), and Maiorana (1978) have presented theoretical arguments which support the existence of size gradations; however, the Hutchinsonian value does not have any theoretical precedence over other values in their analyses.

Roth (1981) succinctly stated that "the study of competition and coexistence can continue without propagating myths about magic numbers", and suggests the use of statistical analyses to ascertain the validity of the "1.26 rule". Ratios from the Caatingas and Cerrado bat communities varied from 1.01 to 1.37. The results of the Behrens-Fisher *t'* Test (Snedecor & Cochran 1967) overwhelmingly indicate that the Hutchinsonian ratio of 1.26 is uncommon among bats; less than 15% of the observed ratios were statistically indistinguishable from 1.26 (Table 4). Further, even if the 1.26 rule is interpreted to indicate a minimum difference beyond which competitive interactions lead to divergence or extinction (see Enders 1976, Van Valen 1978, Pearson & Murry 1979), the rule is not, in general, applicable to bat communities from the northeast of Brazil. Fourteen or approximately two-thirds of the observed ratios were less than, and statistically different from 1.26. Tamsitt (1967) originally suggested that Neotropical bats may tolerate ratios smaller than 1.26; consistent with the conclusion of Simberloff & Broecklen (1981), the Hutchinsonian value certainly does not have any special significance in defining limiting similarity in the Caatingas or edaphic Cerrado faunas.

Some patterns do emerge from the data once the mythical importance of the 1.26 value is put aside. In general, larger ratios occur at the high end of the size gradient,

TABLE 4

Results of the Behrens-Fisher t' Test[1] comparing observed mean forearm size ratios between adjacent sized species of bats in Caatingas and edaphic Cerrado communities to the Hutchinsonian ratio of 1.26. Feeding guild codes as in Table 1, species codes as in Figure 2 to 7.

Resultados de la prueba t' de Behrens-Fisher, comparando los cocientes de tamaño medio del antebrazo observado entre especies contiguas (en el eje de tamaños) de murciélagos de la Caatinga y el Cerrado edáfico, contra el cociente Hutchinsoniano de 1.26. Los códigos para los gremios tróficos están en la Tabla 1; los códigos para las distintas especies son como en las Figuras 2 a la 7.

COMMUNITY	GUILD	BAT SPECIES	SAMPLE SIZE n_1,n_2	FOREARM RATIO $\overline{X}_1/\overline{X}_2$	t'^1	SIGNIFICANCE p
Caatingas	AERIN	PMACR-MNIGR	22,76	1.25	−0.50	$>.50$ NS
Cerrado	AERIN	EFURI-MNIGR	22,76	1.18	−4.50	$\ll.001$ ***
Caatingas	FOLGL	MMEGA-MMINU	14,10	1.03	−8.12	$\ll.001$ ***
		TBRAS-MMEGA	8,14	1.19	−2.80	$< .05$ *
		MCREN-TBRAS	7,8	1.12	−5.41	$< .01$ **
		TSILV-MCREN	49,7	1.26	−0.17	$> .050$ NS
Cerrado	FOLGL	MMEGA-MMINU	14,10	1.03	−8.14	$\ll.001$ ***
Caatingas	OMNIV	PHAST-TCIRR	48,35	1.35	−6.43	$\ll.001$ ***
		TCIRR-PDISC	35,66	1.01	18.89	$\ll.001$ ***
Cerrado	OMNIV	PHAST-PDISC	48,66	1.37	8.07	$\ll.001$ ***
Caatingas	NECTA	GSORI-LMORD	80,72	1.02	−15.44	$\ll.001$ ***
		AGEOF-GSORI	65,80	1.20	−3.68	$\ll.001$ ***
Cerrado	NECTA	AGEOF-GSORI	65,80	1.20	−3.68	$\ll.001$ ***
Caatingas	FRUGI	VLINE-CPERS	48,80	1.11	−8.53	$\ll.001$ ***
		AJAMA-VLINE	40,40	1.25	−0.45	$> .50$ NS
		ALITU-AJAMA	80,40	1.20	−4.23	$\ll.001$ ***
Cerrado	FRUGI	CPERS-SLILI	80,29	1.01	−13.71	$\ll.001$ ***
		VLINE-CPERS	40,80	1.09	−10.50	$\ll.001$ ***
		ACONC-VLINE	12,40	1.01	−12.51	$\ll.001$ ***
		AJAMA-ACONC	40,12	1.21	−1.98	$> .05$ NS
		ALITU-AJAMA	80,40	1.24	−1.46	$> .10$ NS
Caatingas	MOLOS	MMOLO-NMATT	80,48	1.34	4.16	$\ll.001$ ***

[1] $$t' = \left\{X_1 - (1.26)\overline{X}_2\right\} \Big/ \left\{\frac{S_1^2}{n_1} + (1.59)\frac{S_2^2}{n_2}\right\}^{1/2}$$

whereas smaller values occur at the low end of the size gradient. Schoener (1974) presented theoretical arguments for such an expectation (see also Oksanen *et al.* 1979 and Wiens & Rotenbery 1980). Ideally, correlation analysis should be performed on each guild because the relation between size ratio and position on the size gradient may differ among feeding guilds. Since the number of species pairs would, however, be small within guilds, an alternative approach is to pool species pairs from all guilds in order to increase the sample size. Correlation analysis (Sokal & Rohlf 1981) indicates that there is a statistically significant positive association between the position a pair of potential competitors occupies on the size gradient (measured by mean forearm size of the pair) and the observed ratio of forearm sizes ($r=0.45$; df $= 20$; $0.01 < P < 0.05$). The low value of Pearson's r can be attributed, in part to the pooling of data from different guilds in which the particular relation between forearm ratio and size should vary. Insectivorous birds and lizards are also known to exhibit larger ratios with increasing body size (Schoener 1965, 1968). Hence, if morphology does reflect ecology, larger bats may consume a greater variety of food sizes than smaller bats. This could be caused by a possible differential abundance of food items (i.e., large food may be rarer than small foods) which forces larger bats to include a greater range of food sizes in their diet. A qualitative assessment of fruit abundances from both Caatingas and Cerrado biomes suggests that larger fruits are rarer than small fruits, but such measures need to be evaluated quantitatively and applied to other resources as well.

Although the measures of morphological variability do not overlap for most bat species, it is instructive to examine in more detail some of the cases in which overlap does occur. Among nectarivores, *Glossophaga soricina* and *Lonchophylla mordax* are very similar morphologically and measures of individual variability overlap considerably (Fig. 3). Further, *G. soricina* is ubiquitous in the Caatingas, occurring in all habitats where *L. mordax* is found. Although these species potentially would frequently encounter each other in competitive situations, it appears that the effects of competition are reduced because almost all examined specimens of *G. soricina* exclusively consume fruit throughout the year in the Caatingas. This effectively shifts *G. soricina* into the frugivore guild in terms of its ecological impact in the Caatingas. Examination of Fig. 4 indicates that if *G. soricina* were considered to be frugivorous, it would occupy a position on the size gradient to the left of *Carollia perspicillata,*

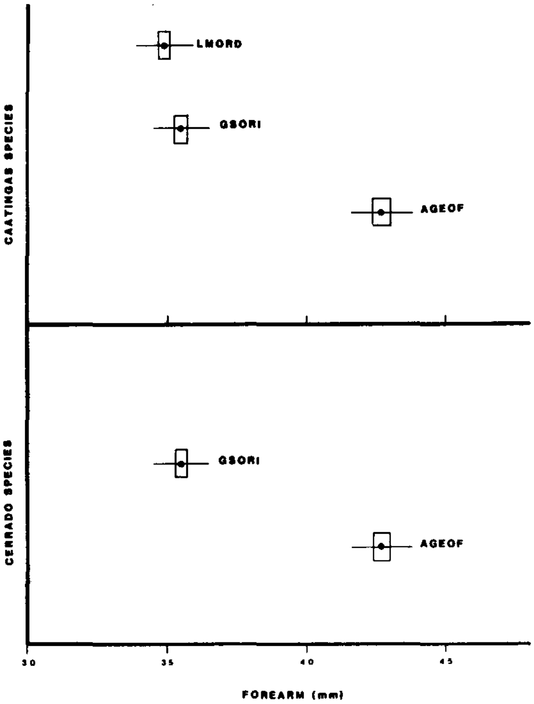

Fig. 3. Size relations among nectarivore species in Caatingas and edaphic Cerrado communities. Mean forearm size is indicated by a solid black dot; 95% Confidence Intervals for mean forearm size are indicated by open horizontal bars; individual variation in forearm size ($\bar{x} \pm$ ISD) is indicated by a solid horizontal line. Size ratios (based upon $\bar{x}$) for successive pairs of species beginning at the left of the $\bar{x}$-axis are 1.02 and 1.20 in the Caatingas, and 1.20 in the Cerrado. Species codes: GSORI = *Glossophaga soricinia,* LMORD = *Lonchophylla mordax,* AGEOF = *Anoura geoffroyi.*

Relaciones del tamaño corporal entre especies de murciélagos nectarívoros de la Caatinga y el Cerrado edáfico. El tamaño medio del antebrazo se indica con un círculo negro; el intervalo de confianza del 95% en torno a la media para tamaño del antebrazo se indica con una barra horizontal; la variación individual en el tamaño del antebrazo ($\bar{x} \pm 1$ DE) se indica con una línea horizontal. Los cocientes de tamaño (basados en $\bar{x}$) para pares de especies contiguas a partir del origen del eje de abscisas son: 1.02 y 1.20 en la Caatinga y 1.20 en el Cerrado. Códigos específicos: GSORI = *Glossophaga soricina,* LMORD = *Lonchophylla mordax,* AGEOF = *Anoura geoffroyi.*

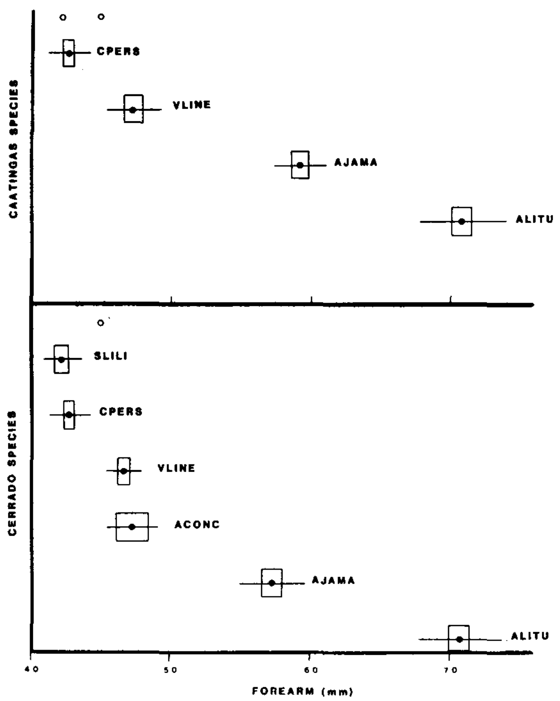

Fig. 4. Size relations among frugivore species in Caatingas and edaphic Cerrado communities. Mean forearm size is indicated by a solid black dot; 95% Confidence Intervals for mean forearm size are indicated by open horizontal bars; individual variation in forearm size ($\bar{x}$ ± ISD) is indicated by a solid horizontal line. Size ratios (base upon $\bar{x}$) for successive pairs of species beginning at the left of the x-axis are 1.11, 1.25 and 1.20 in the Caatingas, and 1.01, 1.09, 1.01, 1.21 and 1.24 in the Cerrado. Uncommon species are indicated by open dots. Species codes: VLINE = *Vampyrops lineatus,* CPERS = *Carollia perspicillata,* AJAMA = *Artibeus jamaicensis,* ALITU = *Artibeus lituratus,* SLILI = *Sturnira lilium,* ACONC = *Artibeus concolor.*

Relaciones del tamaño corporal entre especies de murciélagos frugívoros de la Caatinga y el Cerrado edáfico. El tamaño medio del antebrazo se indica con un círculo negro; el intervalo de confianza del 95% en torno a la media para tamaño del antebrazo se indica con una barra horizontal; la variación individual en el tamaño del antebrazo ($\bar{x}$ ± 1 DE) se indica con una línea horizontal. Los cocientes de tamaño (basados en $\bar{x}$) para pares de especies contiguas a partir del origen del eje de abscisas son: 1.11, 1.25 y 1.20 en la Caatinga y 1.01, 1.09, 1.01, 1.21 y 1.24 en el Cerrado. Las especies no comunes están indicadas con círculos blancos. Códigos específicos: VLINE = *Vampyrops lineatus,* CPERS = *Carollia perspicillata,* AJAMA = *Artibeus jamaicensis,* ALITU = *Artibeus lituratus,* SLILI = *Sturnira lilium,* ACONC = *Artibeus concolor.*

and there would not be any size overlap between them. Hence a potential competitive situation is averted and the importance of considering guild membership as ecological potentials rather than limitations is reinforced.

The apparent occupation of the same size niche by *Sturnira lilium* and *Carollia perspicillata* in the edaphic Cerrado frugivore guild also presents theoretical difficulties (see Fig. 4). However, the genus *Sturnira* (formerly in the subfamily Sturninae) has dental adaptations which enable it to specialize on unripe or extremely hard fruits (Vaughan 1970). Thus, competition between *S. lilium* and *C. perspicillata* may be diminished by each species consuming fruits at different stages of ripeness.

Similarly, *Phyllostomus discolor* and *Trachops cirrhosus* are indicated as potential competitors in the Caatingas omnivore guild (Fig. 3). *Trachops cirrhosus* appears to be primarily animalivorous whereas *P. discolor* is frugivorous for the most part. As a result, competition between these omnivores would, under most circumstances, be negligible.

Two other occurrences of appreciable overlap between species exist in the chiropteran communities from the northeast. Among the frugivores (Fig. 4), *Artibeus concolor* and *Vampyrops lineatus* are potential competitors in the Cerrado; *Micronycteris minuta* and *M. megalotis* co-occur in both Caatingas and Cerrado habitats (Fig. 5). Mechanisms whereby these species pairs avoid the deleterious affects of competition are unknown and remain as questions for future research.

Finally, the role of uncommon bats in ecological communities is unclear and will probably remain so due to the inherent difficulties of capturing rare specimens in sufficient quantity. If these species do play an important role in determining community structure, certain guilds such as the molossid insectivores and the aerial insectivores will be problematic because of the amount of size overlap among component species (see Figs. 6 and 7). Fortunately, however, until indicated otherwise, the effect of a species on community structure is probably related to its abundance in the community, and so rare species may not play an appreciable role in determining community organization (see Bowers & Brown 1982).

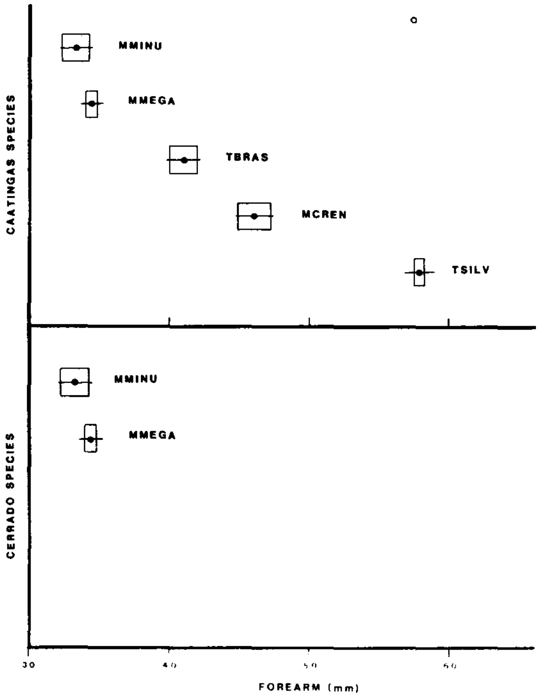

Fig. 5. Size relations among foliage gleaners in Caatingas and edaphic Cerrado communities. Mean forearm size is indicated by a solid black dot; 95% Confidence Intervals for mean forearm size are indicated by open horizontal bars; individual variations in forearm size (x̄ ± ISD) is indicated by a solid horizontal line. Size ratios (based upon x̄) for successive pairs of species beginning at the left of the x-axis are 1.03, 1.19, 1.12 and 1.26 in the Caatingas and 1.03 in the Cerrado. Uncommon species are indicated by open dots. Species codes: MMEGA = *Micronycteris megalotis,* MMINU = *Micronycteris minuta,* TBRAS = *Tonatia brasiliense,* MCREN = *Mimon crenulatum,* TSILV = *Tonatia silvicola.*

Relaciones del tamaño corporal entre especies de murciélagos buscadores en dosel de la Caatinga y el Cerrado edáfico. El tamaño medio del antebrazo se indica con un círculo negro; el intervalo de confianza del 95% en torno a la media para tamaño del antebrazo se indica con una barra horizontal; la variación individual en el tamaño del antebrazo (x ± 1 DE) se indica con una línea horizontal. Los cocientes de tamaño (basados en x̄) para pares de especies contiguas a partir del origen del eje de abscisas son: 1.03, 1.19, 1.12 y 1.26 en la Caatinga y 1.03 en el Cerrado. Las especies no comunes están indicadas con círculos blancos. Códigos específicos: MMEGA = *Micronycteris megalotis,* MMINU = *Micronycteris minuta.* TBRAS = *Tonatia brasiliense,* MCREN = *Mimon crenulatum,* TSILV = *Tonatia silvicola.*

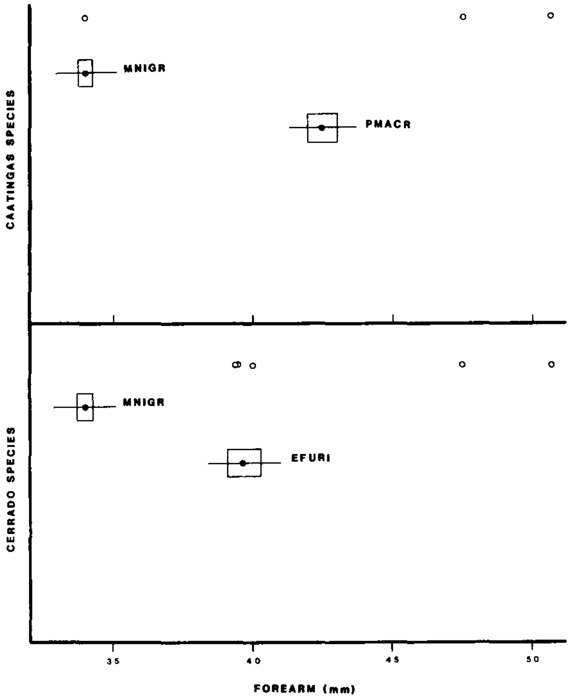

Fig. 6. Size relations among aerial insectivores in Caatingas and edaphic Cerrado communities. Mean forearm size is indicated by a solid black dot; 95% Confidence Intervals for mean forearm size are indicated by open horizontal bars; individual variation in forearm size (x̄ ± ISD) is indicated by a solid horizontal line. Size ratios (based upon x̄) for successive pairs of species beginning at the left of the x-axis are 1.25 in the Caatingas and 1.18 in the Cerrado. Uncommon species are indicated by open dots. Species codes: MNIGR = *Myotis nigricans,* PMACR = *Peropteryx macrotis,* EFURI = *Eptesicus furinalis.*

Relaciones del tamaño corporal entre especies de murciélagos insectívoros aéreos de la Caatinga y el Cerrado edáfico. El tamaño medio del antebrazo se indica con un círculo negro; el intervalo de confianza del 95% en torno a la media para tamaño del antebrazo se indica con una barra horizontal; la variación individual en el tamaño del antebrazo (x ± 1 DE) se indica con una línea horizontal. Los cocientes de tamaño (basados en x̄) para pares de especies contiguas a partir del origen del eje de abscisas son: 1.25 en la Caatinga y 1.18 en el Cerrado. Las especies no comunes están indicadas con círculos blancos. MNIGR = *Myotis nigricans,* PMACR = *Peropteryx macrotis,* EFURI = *Eptesicus furinalis.*

It is clear however, that at least for Caatingas and Cerrado bat communities. Hutchinson's ratio is neither a constant nor minimum measure of species disimilarity. Rather, correlation analysis suggests that dissimilarity between adjacent-sized competitors increases as competitor size increases.

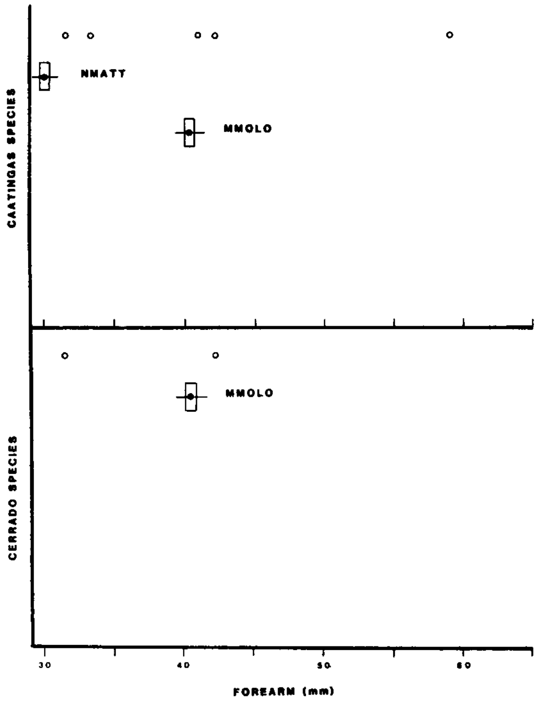

Fig. 7. Size relations among molossid insectivores in Caatingas and edaphic Cerrado communities. Mean forearm size is indicated by a solid black dot; 95% Confidence Intervals for mean forearm size are indicated by open horizontal bars; individual variation in forearm size ($\bar{X}$ ± ISD) is indicated by a solid horizontal line. Size ratio (based upon $\bar{X}$) for successive pairs of species beginning at the left of the x-axis is 1.34 in the Caatingas. Uncommon species are indicated by open dots. Species codes: NMATT = *Neoplatymops mattogrossensis,* MMOLO = *Molossus molossus.*

Relaciones del tamaño corporal entre especies de murciélagos insectívoros molóssidos de la Caatinga y el Cerrado edáfico. El tamaño medio del antebrazo se indica con un círculo negro; el intervalo de confianza del 95% en torno a la media para tamaño del antebrazo se indica con una barra horizontal; la variación individual en el tamaño del antebrazo ($\bar{X}$ ± 1 DE) se indica con una línea horizontal. El cociente de tamaño (basado en $\bar{X}$) para pares de especies contiguas a partir del origen del eje de abscisas es 1.34 en la Caatinga. Las especies no comunes están indicadas con círculos blancos. Códigos específicos: NMATT = *Neoplatymops mattogrossensis,* MMOLO = *Molossus molossus.*

This pattern could be affected by the stochastic assembly of species from available faunal pools or deterministic processes (interspecific competitions is not the only possible deterministic process). Our present understanding of South American bat communities is an ecclectic combination of extrapolations from other areas in the tropics or from studies above the community level. Until additional long-term ecological studies of bat populations within the confines of local communities are completed, knowledge of chiropteran community structure, its ubiquity, and its determinants will remain conjectural. Autecological studies, especially those involving food habits and habitat utilization are desperately needed from South American sites if this ecological vacuum is to be filled with meaningful data.

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